Common Garden Experiments Reveal Uncommon Responses across Temperatures, Locations, and Species of Ants

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Running Title: Uncommon geographic ant warming responses

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ABSTRACT

Population changes and shifts in geographic range boundaries induced by climate change have been documented for many insect species. On the basis of such studies, ecological forecasting models predict that, in the absence of dispersal and resource barriers, many species will exhibit large shifts in abundance and geographic range in response to warming. However, species are composed of individual populations which may be subject to different selection pressures and therefore may be differentially responsive to environmental change. Consequently, asystematic responses across populations and species to warming will alter ecological communities differently across space. Common garden experiments can provide a more mechanistic understanding of the causes of compositional and spatial variation in responses to warming because such experiments are useful for determining if geographically separated populations and co-occurring species respond differently to warming, and they provide the opportunity to compare effects of warming on fitness (survivorship and reproduction). We exposed colonies of two common ant species in the eastern US, *Aphaenogaster rudis* and *Temnothorax curvispinosus*, collected along a latitudinal gradient from Massachusetts to North Carolina, to growth chamber treatments that simulated current and projected temperatures in central Massachusetts and central North Carolina within the next century. Regardless of source location, colonies of *A. rudis*, a keystone seed disperser, experienced high mortality and low brood production in the warmest temperature treatment. Colonies of *T. curvispinosus* from cooler locations experienced increased mortality in the warmest rearing temperatures, but colonies from the warmest locales did not. Our results suggest that populations of some common species may exhibit uniform declines in response to warming across their geographic ranges, whereas other species will respond differently to warming in different parts of their geographic ranges. Our

43 results suggest that differential responses of populations and species must be incorporated into
44 projections of range shifts in a changing climate.
45

INTRODUCTION

The majority of forecasts of the responses of species to climatic warming assume that populations within a species are homogeneous and thus model shifts in the geographic distributions of entire species (but see Buckley 2008; Richardson *et al.* 2011 for exceptions). Likewise, most empirical studies of recent responses to warming focus on individual species and/or locations (but see Pelini *et al.* 2011a) as invariant units of analysis. However, the rate, magnitude, and direction of the responses to warming or other climatic changes by different individuals in different populations of any given species may differ for at least two reasons. First, populations may be locally adapted to current or historical environmental conditions (Gilman *et al.* 2006; Pelini *et al.* 2009; Angert *et al.* 2011). Second, individuals from different populations may differ in their ability to cope with local environmental changes (Magnani 2009). For these reasons, models based on the assumption of uniform responses among populations within a species may be misleading.

The methods necessary to assess if populations are locally adapted to climate or can cope with, or even benefit from climatic change are well established (reviewed in Kawecki & Ebert 2004). The first step is to determine experimentally whether and how individuals from distinct populations vary in their ability to respond to common conditions (Grosholz 2001; Castañeda *et al.* 2005; Pelini *et al.* 2009; Tack & Roslin 2010; Craig *et al.* 2011). The second step is to conduct common garden experiments with treatments that represent different climatic regimes. Three broad outcomes are possible. First, all populations might exhibit increased survivorship or reproduction in response to warming. Second, populations might exhibit local adaptation to historical conditions, or have narrow physiological tolerances, thereby leading to population declines or extinctions under warming. Third, local populations may respond idiosyncratically to

69 warming, with some populations exhibiting local adaptation/narrow physiological tolerances and
70 declining in response to temperature increases, whereas other populations cope with and/or
71 increase in response to temperature increases. All of these outcomes are possible because
72 individuals are behaviorally or phenotypically plastic and populations of individuals possess
73 genetic variation in traits that maximize fitness for different individuals in different conditions.

74 In this study, we used ants to examine variation among populations and co-occuring species
75 under expected temperature change in the eastern United States (also see Fitzpatrick *et al.* 2011;
76 Jenkins *et al.* 2011). Ants are an ideal taxon to use for multiple common-garden experiments
77 because they are responsive to temperature (Dunn *et al.* 2009) and relatively easy to maintain in
78 controlled environments. Temperature is correlated with patterns of ant diversity and abundance
79 (Sanders *et al.* 2007), seasonal patterns of activity (Dunn *et al.* 2007), overwintering mortality
80 (Sorvari *et al.* 2011), foraging behavior (Ruano *et al.* 2000), and the outcomes of interactions
81 between species (Cerda *et al.* 1997; Holway *et al.* 2002). Ant foraging activities modulate many
82 ecosystem processes, including decomposition, nutrient cycling, and primary production
83 (Hölldobler & Wilson 1990; Folgarait 1998; Del Toro *et al*. In press). Consequently, the extent
84 to which ants respond to climatic change, especially to local and regional changes in
85 temperature, may have cascading consequences for other taxa and for ecosystem dynamics
86 (Lensing & Wise 2006; Moya-Larano & Wise 2007). Other work has demonstrated that ant
87 community responses to warming differ across latitude (Pelini *et al*. 2011a), making ants an ideal
88 taxon for examining the underlying causes of geographic variation in the ecological responses to
89 climate change.

90 Using a common garden experiment, we tested the hypothesis that the relationship between
91 temperature and fitness will vary for ant populations sampled across a species' range. In order to

understand if patterns in intraspecies variation in temperature impacts on fitness are generalizable, we tested the hypothesis that co-occuring, closely related species with similar geographic distributions would display similar patterns in intraspecies variation in their response to varying temperature; this is one of the first studies to experimentally test this hypothesis. Growth chamber studies are particularly useful for examining insect responses to warming because they circumvent heat- island effects associated with warming treatments applied in the field (Moise & Henry 2010). We placed ant colonies in growth chambers set to summer temperatures in the regions from which ants were collected as well as to mimic summer temperatures in the future (Solomon *et al.* 2007). To determine if ants from different climates differed in their ability to cope with shifts in temperature, and more generally to determine if warming could have a net negative or positive effect on populations across the geographic ranges of species, we examined associations between source location mean summer temperature and experimental rearing temperature on two measures of fitness: survival and brood production. Fitness differences attributed to source location temperatures would suggest that individuals from different locations differed in their ability to cope with temperature change. Increases in fitness with increases in rearing temperature would suggest that populations throughout species' ranges will have increased fitness under warming, whereas decreases would suggest that warming will have negative fitness effects across species' ranges. Fitness differences attributed to interactions between source location temperatures and rearing temperature would suggest that populations from different locales are affected differently by temperature shifts.

METHODS

Common garden

The focal taxa for these experiments were populations of *Aphaenogaster rudis* Mayr and *Temnothorax curvispinosus* Mayr from Massachusetts to North Carolina (33.6 - 42.5°; Table 1). These two ant species co-occur across forests in the eastern US (Pelini *et al.* 2011a). While *T. curvispinosus* is recognized as a species (Mackay 2000), *A. rudis* is a species complex (Umphrey 1996) currently undergoing taxonomic revision (Bernice DeMarco, *unpublished data*). In order to determine if patterns observed in our focal species were similar to those for other species, we also included a subset of colonies of other species that co-occur with the focal species: *A. fulva* Roger, *Camponotus chromaiodes* Bolton, *Crematogaster lineolata* Say, *Tapinoma sessile* Say, and *Temnothorax longispinosus* Roger (Table 1). We placed single queen colonies in artificial nest boxes and allowed them to acclimate to laboratory conditions for two weeks before placing them into growth chambers at North Carolina State University lab facilities. Artificial nests were plastic containers ($390cm^3$) with sand, water tubes plugged with cotton (to maintain humidity), and a food source (Bhatkar & Whitcomb 1970). When brood or males were collected with the colonies, we removed them so as to assess more accurately survival and reproductive output of the colony throughout the duration of the experiment.

We placed colonies in their artificial nest boxes into one of three growth chamber temperature treatments, with temperatures determined from long-term temperature records from Harvard Forest, Massachusetts (21˚C summer mean); Duke Forest, North Carolina (26˚C summer mean) and Miami, Florida (31˚C summer mean); the 26˚C treatment represents projected warming for Massachusetts before 2100, and the warmest treatment, 31˚C, represents the forecast temperature for Massachusetts beyond 2100 and for North Carolina before 2100 (Solomon *et al.* 2007). Chamber temperatures fluctuated diurnally, i.e., temperatures were ramped up/down by 1.2˚C per hour) between the average minimum (at 3am) and maximum (at 3pm) temperatures for each

location (Massachusetts: 16-26˚C; North Carolina: 21-31˚C; Florida: 26-36˚C), and day-length was 14 hours long in all chambers.

We checked nests daily to ensure constant water and food supply. We censused ant colonies in July before transferring them to the growth chambers, again 10 days after the start of the experiment, and finally at the end of the experiment in September (59 days total). At each census, we recorded the presence or absence of brood and the number of workers in each colony.

Data analysis

First, we used generalized linear mixed models (R version 2.9.0; R Development Core Team 2007) to test whether survival and brood production (binomial response variables) were significantly affected by source-location temperature (fixed effect) and/or rearing temperature (fixed effect), across all species (random effect) and both census periods (random effect). To determine if patterns found across our entire species pool were consistent with those for the focal species, *Aphaenogaster rudis* and *Temnothorax curvispinosus,* for which we had broader geographic coverage, we ran similar models examining the effects of source-location temperature, rearing temperature, and species as fixed effects, and census period as a random effect. We also included a species × source-location temperature term to determine if the ability of colonies from different source locations to cope with temperature change was similar in both focal species. In addition, we also included a species × rearing temperature term in this model to determine if the two focal species differed in their responses to rearing temperature, regardless of source location. Lastly, because both species × source-location temperature and species × rearing temperature had significant effects on survival of the two focal species, we examined in more detail the separate responses of *A. rudis* and *T. curvispinosus.* For each of these two species, we

159 modeled survival as a function of source-location temperature, rearing temperature and their
160 interaction. Significant interactions between source-location temperature and rearing temperature
161 revealed if colonies from different locales were affected differently by similar temperatures,
162 which may be due to adaptive differences such as local adaptation. We extracted the mean
163 summer (warmest quarter) temperatures at the source locations from WorldClim (Hijmans *et al.*
164 2005).

165

166 RESULTS

167 Interspecies Models—Survival decreased with increasing rearing temperature (all species:
168 χ^2=5800; P<0.001; focal species: χ^2=3800; P<0.001) but increased with source-location
169 temperature (all species: χ^2=4.3; P=0.037; focal species: χ^2=500; P<0.001) (Figure 1). Brood
170 production also decreased with increasing rearing temperature (all species: χ^2=19; P<0.001; focal
171 species: χ^2=18; P<0.001). In our focal species model of survival, the species × source-location
172 temperature and species × rearing temperature terms also were significant (χ^2=1900; P<0.001;
173 χ^2=6000; P<0.001, respectively).

174 Intraspecies Models—Survival of both *Aphaenogaster rudis* and *Temnothorax curvispinosus*
175 decreased with increasing rearing temperature (χ^2=120; P<0.001 and χ^2=36; P<0.001,
176 respectively) but increased with source-location temperature (χ^2=200; P<0.001 and χ^2=17;
177 P<0.001, respectively) (Figure 1, lower panels). Interactions between source-location and rearing
178 temperature also were significant, but different, for both species (*A. rudis*: χ^2=270; P<0.001 and
179 *T. curvispinosus*: χ^2=30; P<0.001). More specifically, *A. rudis* colonies from warmer locations
180 had higher survival than those from cooler locations in the low and intermediate rearing

temperatures, but all colonies had high mortality in the warmest rearing temperature (Figure 2, upper panel). In contrast, *T. curvispinosus* colonies from different source locations did not differ significantly in survival except in the warmest rearing temperature, where colonies from two of the three warmest source locations had relatively high survival compared to their cooler source-location counterparts (Figure 2, lower panel).

DISCUSSION

Species are composed of individual populations, which may be subject to different selection pressures. Some will go extinct locally or globally, some will migrate, and some will increase in size (Pelini *et al.* 2009). Increasing temperatures may have negative fitness effects for populations that are locally adapted to and/or have narrow physiological tolerances of temperature and positive fitness effects for other populations with broader physiological tolerances of temperature. If different populations respond differently to climatic warming, then extrapolating to a single, overall response of the given species may be unwise or unwarranted. Furthermore, a species' potential to adapt to future climatic change may be reduced if some populations perform well while others decline under warming and causes a reduction in genetic diversity (Collevatti 2011). In aggregate (at the species level), all eight ant species that we studied in this common garden experiment exhibited decreased survival and brood production with increased warming. However, we observed strong differences among species and populations within particular species. Colonies of both focal species, *Temnothorax curvispinosus* and *Aphaenogaster rudis,* from warmer locales had higher survival and brood production under warmer temperatures than those from cooler sites. Survival decreased with increasing

203 temperatures for *A. rudis* from all locales. The results for *T. curvispinosus* were very similar,
204 with one exception: colonies of *T. curvispinosus* from the warmest locale experienced increased
205 fitness in the warmer temperatures. Together, these findings suggest that for many of the species
206 in our study system, warming may be detrimental. However, where responses differ among
207 populations within species, warming affects southern populations (from warmer climates) less
208 than it does northern populations (from cooler climates). This latter result suggests that
209 forecasted distributions of ant species in a warmed world, whether based on physiology or
210 distributional data, do not account for intraspecific variability and may be inaccurate.

211 Because *A. rudis* populations responded negatively to temperature increases regardless of their
212 location of origin, we forecast that severe warming will negatively affect populations of this
213 species across its entire range. As the primary disperser of many forest understory herbs (Ness *et*
214 *al.* 2009), reductions in *Aphaenogaster* populations are likely to have ramifying consequences in
215 many forests (e.g., Rodriguez-Cabal *et al*. 2012). Unlike *A. rudis*, *T. curvispinosus* colonies from
216 warmer, southern locales performed well under warming whereas their counterparts from cooler,
217 northern locales did not. Southern *T. curvispinosus* populations may have more genetic diversity
218 in traits related to physiological tolerances than northern colonies. We also observed noticeably
219 increased foraging activity in *Aphaenogaster rudis* (S. Diamond, personal observation) and
220 running speeds in *Temnothorax curvispinosus* (H. MacLean, unpublished data) in the warmer
221 temperature treatments, suggesting that some of the mortality associated with warming may be
222 due to changes in behavioral and physiological traits (e.g., Dillon et al. 2010).

223 The findings from this laboratory common garden experiment complement those from recent
224 field warming manipulations in the same system with many of the same ant species. In field
225 warming experiments, we found increases in abundance under warming up to 5°C for low

latitude (North Carolina) populations of species with higher thermal tolerances, including *Crematogaster lineolata* (and see Pelini *et al.* 2011a) and *T. curvispinosus*, but not for *Aphaenogaster rudis* and other species with lower thermal limits. Abundances of species at a higher latitude site (Massachusetts) increased under warming regardless of their thermal tolerances (Diamond *et al*. in review). The data from the laboratory common garden experiment reported here, together with data from our previous field experiments, suggest that the responses of ants to warming will vary across populations within and across species (also see Fitzpatrick *et al.* 2011; Jenkins *et al.* 2011 for modeling of ant communities under climate change).

Future studies should addresses how such changes could have cascading consequences for species interactions and ecosystem processes (Traill *et al.* 2010) that are localized and are not well projected by current models that assume uniform responses of species across their entire range. Multiple observational and experimental approaches should be integrated because complex abiotic (e.g., humidity, rainfall) and biotic (e.g., interactions with predators/prey or plants) changes are associated with climatic change can be captured by field manipulations but separated by common garden laboratory experiments.

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LITERATURE CITED

Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ (2011) Do species' traits predict recent shifts at expanding range edges? *Ecology Letters,* **14,** 677-689.

Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, Roques A, Larsson S (2005) Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecological Applications,* **15,** 2084-2096.

Bhatkar A, Whitcomb WH (1970) Artifical diet for rearing various species of ants. *The Florida Entomologist,* **53,** 4.

Buckley Lauren B (2008) Linking Traits to Energetics and Population Dynamics to Predict Lizard Ranges in Changing Environments. *The American Naturalist,* **171,** E1-E19.

Castañeda LE, Lardies MA, Bozinovic F (2005) Interpopulational variation in recovery time from chill coma along a geographic gradient: A study in the common woodlouse, Porcellio laevis. *Journal of Insect Physiology,* **51,** 1346-1351.

Cerda X, Retana J, Cros S (1997) Thermal disruption of transitive hierarchies in Mediterranean ant communities. *Journal of Animal Ecology,* **66,** 363-374.

Collevatti RG (2011) Range shift and loss of genetic diversity under climate change in *Caryocar brasiliense*, a Neotropical tree species." *Tree Genetics and Genomes*, **7**(6), 1237.

Craig TP, Itami JK, Ohgushi T, Ando Y, Utsumi S (2011) Bridges and barriers to host shifts resulting from host plant genotypic variation. *Journal of Plant Interactions,* **6,** 141-145.

Del Toro I, Ribbions RR, Pelini SL (2012) The little things that run the world revisited: A review of ant-mediated (Hymenoptera: Formicidae) ecosystem services and disservices. *Myrmecological News*, In press.

273 Dillon ME, Wang G, Huey RB (2010) Global metabolic impacts of recent climate warming.
274 *Nature,* **467,** 704-U788.
275 Dunn RR, Agosti D, Andersen AN*, et al.* (2009) Climatic drivers of hemispheric asymmetry in
276 global patterns of ant species richness. *Ecology Letters,* **12,** 324-333.
277 Dunn RR, Parker CR, Geraghty M, Sanders NJ (2007) Reproductive phenologies in a diverse
278 temperate ant fauna. *Ecological Entomology,* **32,** 135-142.
279 Fitzpatrick MC, Sanders NJ, Ferrier S, Longino JT, Weiser MD, Dunn R (2011) Forecasting the
280 future of biodiversity: a test of single- and multi-species models for ants in North
281 America. *Ecography,* **34,** 836-847.
282 Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: a review.
283 *Biodiversity and Conservation,* **7,** 1221-1244.
284 Gilman SE, Wethey DS, Helmuth B (2006) Variation in the sensitivity of organismal body
285 temperature to climate change over local and geographic scales. *Proceedings of the*
286 *National Academy of Sciences of the United States of America,* **103,** 9560-9565.
287 Grosholz E (2001) Small spatial-scale differentiation among populations of an introduced
288 colonial invertebrate. *Oecologia,* **129,** 58-64.
289 Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated
290 climate surfaces for global land areas. *International Journal of Climatology,* **25,** 1965-
291 1978.
292 Hochkirch A, Damerau M (2009) Rapid range expansion of a wing-dimorphic bush-cricket after
293 the 2003 climatic anomaly. *Biological Journal of the Linnean Society,* **97,** 118-127.
294 Hölldobler B, Wilson EO (1990) *The Ants.* Belknap Press, Cambridge, MA.

295 Holway DA, Suarez AV, Case TJ (2002) Role of abiotic factors in governing susceptibility to
296 invasion: A test with argentine ants. *Ecology,* **83,** 1610-1619.
297 Jenkins CN, Sanders NJ, Andersen AN*, et al.* (2011) Global diversity in light of climate change:
298 the case of ants. *Diversity and Distributions,* **17,** 652-662.
299 Kawecki TJ, Ebert D (2004) Conceptual issues in local adaptation. *Ecology Letters,* **7,** 1225-
300 1241.
301 Lensing JR, Wise DH (2006) Predicted climate change alters the indirect effect of predators on
302 an ecosystem process. *Proceedings of the National Academy of Sciences of the United*
303 *States of America,* **103,** 15502-15505.
304 Mackay WP (2000) A review of the New World ants of the subgenus Myrafant, (Genus
305 Leptothorax) (Hymenoptera : Formicidae). *Sociobiology,* **36,** 265-434.
306 Magnani F (2009) Phenotypic variability: underlying mechanisms and limits do matter. *New*
307 *Phytologist,* **184,** 277-279.
308 Moise ERD, Henry HAL (2010) Like moths to a street lamp: exaggerated animal densities in
309 plot-level global change field experiments. *Oikos,* **119,** 791-795.
310 Moya-Larano J, Wise DH (2007) Direct and indirect effects of ants on a forest-floor food web.
311 *Ecology,* **88,** 1454-1465.
312 Ness JH, Morin DF, Giladi I (2009) Uncommon specialization in a mutualism between a
313 temperate herbaceous plant guild and an ant: are Aphaenogaster ants keystone
314 mutualists? *Oikos,* **118,** 1793-1804.
315 Pelini SL, Boudreau M, McCoy N, Ellison AM, Gotelli NJ, Sanders NJ, Dunn RR (2011a)
316 Effects of short-term warming on a low and high latitude forest ant community.
317 *Ecosphere,* **2(5),** art62.

Pelini SL, Bowles FP, Ellison AM, Gotelli NJ, Sanders NJ, Dunn RR (2011b) Heating up the forest: open-top chamber warming manipulation of arthropod communities at Harvard and Duke Forests. *Methods in Ecology and Evolution,* **2,** 534-540.

Pelini SL, Dzurisin JDK, Prior KM, Williams CM, Marsico TD, Sinclair BJ, Hellmann JJ (2009) Translocation experiments with butterflies reveal limits to enhancement of poleward populations under climate change. *Proceedings of the National Academy of Sciences,* **106,** 11160-11165.

Richardson K, Hoffmann AA, Johnson P, Ritchie S, Kearney MR (2011) Thermal Sensitivity of Aedes aegypti From Australia: Empirical Data and Prediction of Effects on Distribution. *Journal of Medical Entomology,* **48,** 914-923.

Rodriguez-Cabal MA, Stuble KL, Guenard B, Dunn RR, Sanders NJ (2012) Disruption of ant-seed dispersal mutualisms by the invasive Asian needle ant (Pachycondyla chinensis). *Biological Invasions*, **14**, 557-565.

Ruano F, Tinaut A, Soler JJ (2000) High surface temperatures select for individual foraging in ants. *Behavioral Ecology,* **11,** 396-404.

Sanders NJ, Lessard JP, Fitzpatrick MC, Dunn RR (2007) Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography,* **16,** 640-649.

Solomon S, Intergovernmental Panel on Climate Change., Intergovernmental Panel on Climate Change. Working Group I. (2007) *Climate change 2007 : the physical science basis : contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge ; New York, viii, 996 p. pp.

Sorvari J, Haatanen M-K, Vesterlund S-R (2011) Combined effects of overwintering temperature and habitat degradation on the survival of boreal wood ant. *Journal of Insect Conservation* **15**, 727-731.

Tack AJM, Roslin T (2010) Overrun by the neighbors: Landscape context affects strength and sign of local adaptation. *Ecology,* **91,** 2253-2260.

Tougou D, Musolin DL, Fujisaki K (2009) Some like it hot! Rapid climate change promotes changes in distribution ranges of Nezara viridula and Nezara antennata in Japan. *Entomologia Experimentalis et Applicata,* **130,** 249-258.

Traill LW, Lim MLM, Sodhi NS, Bradshaw CJA (2010) Mechanisms driving change: altered species interactions and ecosystem function through global warming. *Journal of Animal Ecology,* **79,** 937-947.

Umphrey GJ (1996) Morphometric discrimination among sibling species in the fulva-rudis-texana complex of the ant genus Aphaenogaster (Hymenoptera: Formicidae). *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* **74,** 528-559.

TABLES

Table 1. Source locations (decimal degrees), mean summer temperatures (WorldClim, Hijmans *et al.* 2005) at source locations, and number of colonies placed into three growth chamber temperature treatments from each species. For species x sampling locations with fewer than 3 colonies, priority was given to the intermediate (26°C) and warmest (31°C) temperature treatments. Black text indicates focal species; non-focal species are gray.

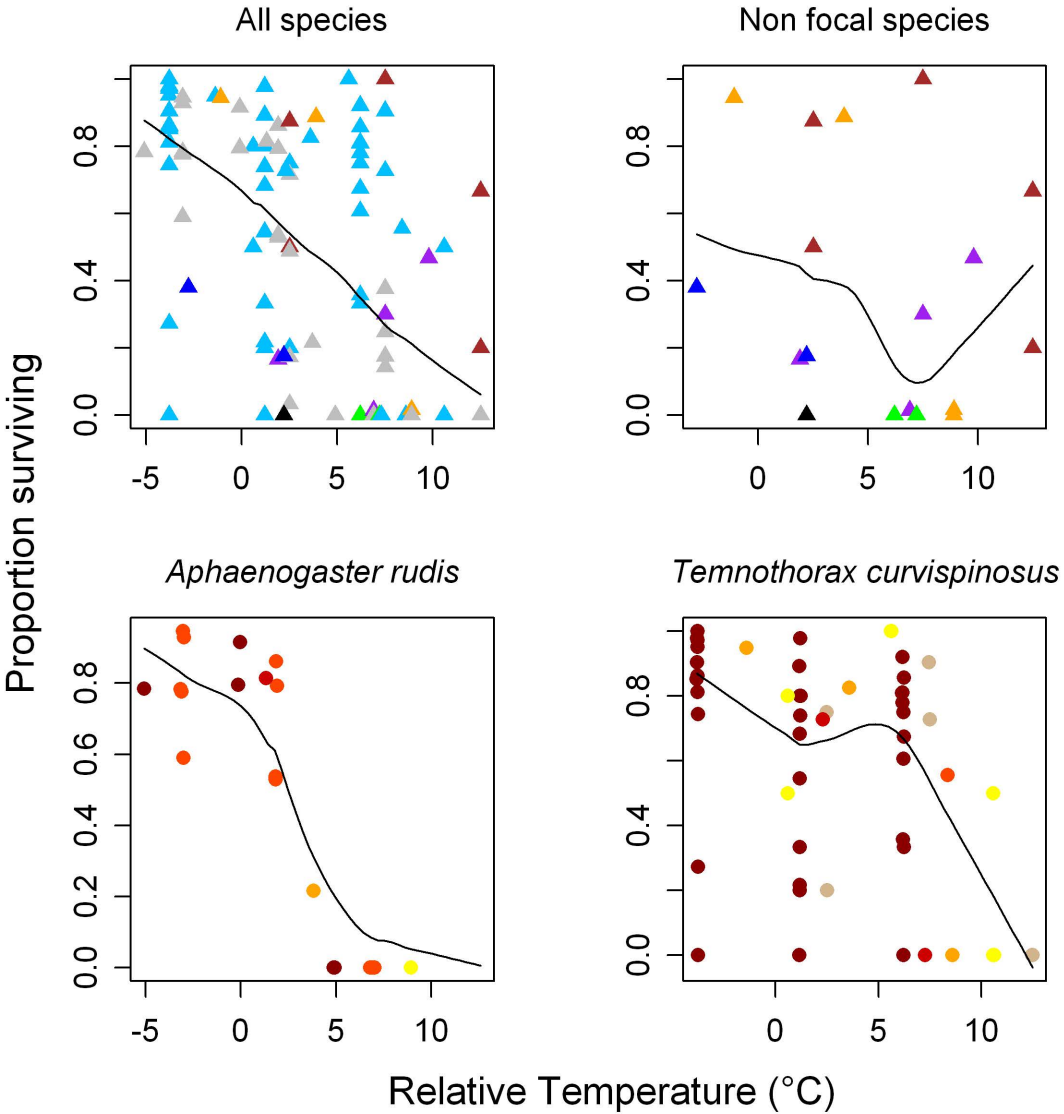
Species	Source locations (decimal degrees)	Mean summer temperature (°C)	Rearing temperature (# colonies)		
			21°C	26°C	31°C
Aphaenogaster rudis	33.63°, −91.79°	26.1	1	2	2
	35.78°, −78.80°	24.8	0	1	0
	36.04°, −79.07°	24.1	5	4	5
	39.89°, −74.58°	22.3	0	1	0
	40.02°, −83.01°	22.1	0	0	1
	42.53°, −72.19°	18.5	4	4	4
Temnothorax curvispinosus	35.76°, −78.68°	24.8	12	11	12
	38.57°, −77.37°	23.7	0	1	1
	39.64°, −74.66°	22.6	0	0	1
	40.44°, −74.27°	22.4	1	1	1
	41.84°, −70.67°	20.4	2	2	3
	42.35°, −72.19°	18.5	2	2	2
Aphaenogaster carolinenesis	35.78°, −78.68°	24.7	0	0	1
	38.51°, −90.83°	23.8	0	0	1
Aphaenogaster fulva	38.51°, −90.83°	23.8	1	1	1
Camponotus chromaiodes	38.51°, −90.83°	23.8	0	1	1
Crematogaster lineolata	36.04°, −79.07°	24.1	0	1	1
	40.58°, −76.75°	21.2	0	1	1
	42.53°, −72.19°	18.5	0	1	0
Tapinoma sessile	38.51°, −90.83°	23.8	0	0	1
	40.02°, −83.01°	22.1	1	1	2
Temnothorax longispinosus	42.53°, −72.19°	18.5	2	1	2

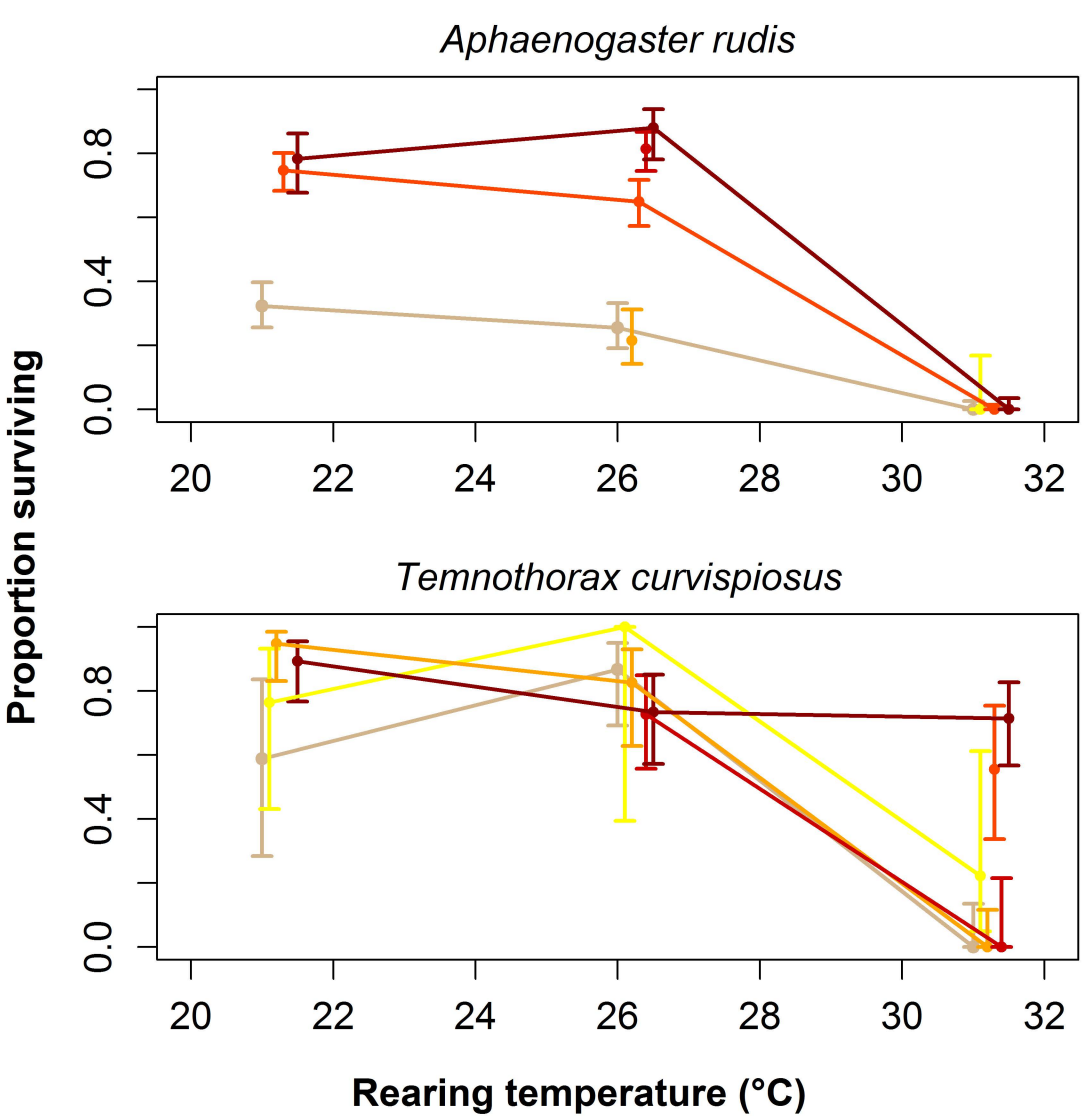
FIGURES

Figure 1. Scatterplots of survival (at final census) as a function of mean rearing temperature - source-location summer temperatures. Upper left panel shows data for all species considered in the experiment; upper right shows all species except for *Aphaenogaster rudis* and *Temnothorax curvispinosus*; lower left shows *A. rudis*; and lower right shows *T. curvispinosus* survival. Positive *x*-axis values indicate cases when experimental temperatures were higher than those at colony source locations, and negative values indicate cases when rearing temperatures were lower. Lines represent locally-weighted scatterplot smoothing (function *loess* in R). In plots with multiple species (upper panels), species are shown in different colors: green = *Aphaenogaster carolinenesis*; blue = *A. fulva*; gray = *A. rudis*; black = *Camponotus chromaiodes*, purple = *Crematogaster lineolata*, orange = *Tapinoma sessile*, light blue = *Temnothorax curvispinosus*; brown = *Temnothorax longispinosus*. For *Aphaenogaster rudis* and *Temnothorax curvispinosus* (bottom panels), colors represent mean summer temperatures at source locations: *A. rudis* - darkred = 26.1°C, red = 24.8°C, orangered = 24.1°C, orange = 22.3°C, yellow= 22.1°C, tan= 18.5°C; *T. curvispinosus* - darkred = 24.8°C, red = 23.7°C, orangered = 22.6°C, orange = 22.4°C, yellow= 20.4°C, tan= 18.5°C.

Figure 2. Mean survival (at final census) of *Aphaenogaster rudis* (upper panel) and *Temnothorax curvispinosus* (lower panel) as a function of rearing temperature. Error bars represent 95% binomial proportion confidence intervals. Lines are colored by source locations such that the coolest location is tan and the warmest is darkred. Colors represent mean summer temperatures at source locations: *A. rudis* - darkred = 26.1°C, orangered = 24.1°C, tan= 18.5°C; *T. curvispinosus* - darkred = 24.8°C, red = 23.7°C, orange = 22.4°C, yellow= 20.4°C, tan=

18.5°C. Points are jittered along the x-axis so that points of overlap between different source locations can be visible. Rearing temperatures were 21°C, 26°C, and 31°C.


All species
Non focal species
Aphaenogaster rudis
Temnothorax curvispinosus
Proportion surviving
Relative Temperature (°C)
0.0
0.2
0.4
0.6
0.8
-5
0
5
10


Aphaenogaster rudis
Temnothorax curvispiosus
Proportion surviving
0.0
0.4
0.8
20
22
24
26
28
30
32
Rearing temperature (°C)